Load Carriage during Foraging in Two Species of Solitary Wasps

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Abstract.—Foraging strategies of two species of solitary digger wasps (Hymenoptera: Crabronidae) were examined. Both species capture insects and return with them in flight to a burrow where they are used as food for larvae. The actual loading of the wasps was compared to a theoretical ideal, the maximum that they should be able to carry in flight. *Bembix troglodytes* Handlirsch is a relatively large wasp that carries many small flies to its burrows. The flies are much smaller than the ideal size, but the choice of small prey appears to be adaptive in that it should reduce the rate of stealing of flies by conspecific females, which was a common event. *Tachytes chrysopyga* Cresson is a relatively small wasp that carries relatively large prey, grasshoppers and crickets, to its burrow. The average size of prey appears to be ideal; however, the distribution of prey size is so great that many wasps were underloaded, while others were overloaded. Prey theft was not observed in *T. chrysopyga*, and flexible flight behaviors (e.g. short, hopping flights) allow it to carry a broad range of prey sizes. These two wasp species may represent near extremes of a continuum of behavior among predaceous wasps.

Although much is now known about the foraging and nest provisioning behaviors of solitary wasps (O'Neill 2001, Evans and O'Neill 2007), their foraging strategies have not been extensively studied using the conceptual framework offered by optimal foraging theory. One approach to examining foraging decisions in such species is to develop a prediction of the optimal load size of the prey, and to test this prediction against the size of actual loads. Fortunately, the maximal load size is simple to calculate for species that carry the prey in flight. Marden (1987) measured the maximum lift force of a variety of flying animals, including 33 bees and wasps, by progressively loading individuals with weights until they could not take off. The force production of flying animals is primarily dependent on their flight muscle mass. In Hymenoptera, this relationship is quite strong ($r^2 = 0.99$), and at the maximum load mass, the ratio of flight muscle mass to body mass (or flight muscle ratio, FMR) is 0.179 (Marden 1987).

Use of flight muscle ratio as a metric for flight capability has several advantages, primarily its independence of the size of the wasp. For wasps that carry their prey in flight, the maximum force produced must equal or exceed the combined weight of the wasp and prey. Assuming it is optimal for a wasp to carry the largest prey possible, the FMR (now flight muscle mass divided by combined body and prey mass) should approach but not exceed 0.179. We have tested this prediction in yellowjackets (*Vespula* spp, Coelho and Hoagland 1995), the eastern cicada killer (*Sphecius speciosus* Drury, Coelho 1997), the great golden digger wasp (*Sphex ichneumoneus* L., Coelho and LaDage 1999), and the carpenter wasp (*Monobia quadridens* L., Edgar and Coelho 2000). In no case yet examined has

the FMR of foraging wasps fallen precisely at the predicted value; however, investigation of the causes for the deviation from "optimality" has always revealed interesting insights into foraging behavior. In this study we apply this method to examine the foraging strategies of two rather different crabronid wasps facing different selection pressures.

Bembix

The general biology of *Bembix* and specific details of *B. troglodytes* Handlirsch, the subject of this study, are described by Evans (1957; 1963). Only relevant aspects of their behavior are summarized here. *Bembix* is a genus of crabronid wasps that hunt flies (Diptera) and carry them to their burrow in flight. The female digs a single burrow in the ground and excavates a nest cell. In progressive provisioners, an egg is laid and attached to the first prey in the cell or to the substrate in the center of the cell. In *B. troglodytes,* oviposition occurs in an empty cell, and the first fly is captured, paralyzed and placed in the cell later (Evans 1957, Evans and O'Neill 2007). The female continues to capture flies and feed them to its developing larva. As the larva increases in size, the rate of provisioning increases (Tengö et al. 1996). A final flurry of foraging provides the larva with all the flies it will require and the female then seals the burrow and digs another. *Bembix* burrows often occur in high-density aggregations, perhaps as a response to parasite and predator pressure, as the relative incidence of parasites per nest decreases with increasing nest density in at least one species (Larsson 1986). *Bembix troglodytes* females close the burrow when leaving it to hunt, but only when the larva is young. The burrow is left open during the intensive foraging phase and closed only at night. *Bembix* exploit the most abundant flies available, apparently learning the richest sources of flies and repeatedly exploiting them (Evans 1957, 1963). *Bembix troglodytes* preys upon a large variety of flower-visiting flies, though most are relatively small in size. Exceptionally small flies are provided to young larvae, while older larvae are provisioned with larger flies. Digging and provisioning a single nest requires only about six days and from 21 to 26 flies are required to fully provision a larva (Evans 1957).

Tachytes

Tachytes is a genus of digger wasps that stocks its underground burrows with Orthoptera carried in flight from foraging areas. *Tachytes* digs complex burrows with multiple cells and packs each cell with up to 10 prey items. The egg is not laid until the cell is fully provisioned (Evans and Kurczewski 1966, Elliot and Salbert 1981), a case of mass provisioning. *Tachytes* nest aggregations are sometimes associated with those of *Sphecius*, as they were in this study. In one species, *T. distinctus* F. Smith, males establish perches near the nest entrance of a female and chase any insect that flies near, including brood parasites such as *Zanysson texanus* (Cresson) (Lin and Michener, 1972).

MATERIALS AND METHODS

We conducted our observations and measurements on a large nesting aggregation of *Bembix troglodytes* Handlirsch at the Hot Springs area of Big Bend National Park (N 29° 10′ 39.57″ latitude, W 102° 59′ 52.73″ longitude, Brewer Co., Texas) from 22 to 23 May 2006. We noted other aggregations, apparently of the same species, at Santa Elena Canyon and Boquillas Canyon, all in sandy areas immediately adjacent to the Rio Grande River. These aggregations were in approximately the same locations as those we observed in previous years. Female wasps carrying prey were netted and weighed on an Ohaus Adventurer-Pro electronic balance to the nearest mg. The head, abdomen, legs and wings of the wasps were removed with scissors and the thorax mass determined. Flight muscle mass was estimated

as 95% of thorax mass (Marden 1987). The mass of the prey fly and its thorax mass were similarly determined. Several of the wasps were collected as voucher specimens and deposited in the Lafayette College Insect Collection and the Quincy University Life Sciences Museum.

We discovered a large colony of *Tachytes chrysopyga obscurus* Cresson nesting on an earthen berm within an even larger aggregation of the eastern cicada killer (*Sphecius speciosus* Drury). This berm was located within a large chemical production facility (Flint Hills Resources) in Will County, IL, at N 41° 26′ 39.31″ latitude, W 88° 10′ 22.16″ longitude. From 27 to 28 July, 2006, female wasps were collected as they returned to their burrows with prey. Body, thorax and prey mass were determined as described above. Several wasps were collected as voucher specimens and deposited with the California Academy of Sciences entomology collection. All prey were deposited in the Quincy University Life Sciences Museum. All data are reported as mean ± standard error unless otherwise indicated. Descriptive statistics were calculated using Microsoft® Excel 2003, while T tests were performed using VassarStats (Lowry 2007).

RESULTS

Bembix troglodytes

Bembix troglodytes females averaged 99 ± 2(N = 48) mg in body mass and 37 ± 0.003(N = 48) mg in thorax mass, resulting in an unladen FMR of 0.36 ± 0.004(N = 48). Fly prey of *B. troglodytes* averaged 45 ± 3(N = 33) mg in body mass and 16 ± 1.1(N = 33) mg in thorax mass, resulting in an FMR of 0.33 ± 0.01(N = 32). Carrying flies resulted in a loaded FMR of 0.29 ± 0.006(N = 27) for female *B. troglodytes* and loaded FMR ranged from 0.23 to 0.34. Hence, all fly-carrying females had FMRs well above the marginal FMR of 0.179 (Fig. 1A).

There was no significant relationship between wasp body mass and prey body mass in *B. troglodytes*. However, small wasps were restricted to the smallest flies, while larger wasps carried a greater range of sizes of flies (Fig. 2A).

There were usually many wasps flying about the nest aggregation, some of which were doubtlessly males engaged in the sun dance (Evans 1957). Many, however, were females. As successful hunters returned to the aggregation, they were nearly always pounced upon by conspecifics before they had the opportunity to land. Often the prey was dropped, and then picked up by the same or another female. Prey-laden females were fast, maneuverable, surprisingly difficult to distinguish from unladen females, and difficult to catch. The fly was tucked under the body and held tightly with all legs. A slightly larger profile normally provided the investigator with the cue that a wasp was carrying prey. *Bembix troglodytes* with prey generally landed and entered their burrows very rapidly if they escaped attempts at prey theft.

Digging activity was frequent. The thistledown velvet ant (*Dasymutilla gloriosa* (Sauss.)), a brood parasite, was common in the area, and often observed digging in the sand as well as entering open burrows. Brood parasitic satellite flies were frequently observed perched at nest entrances and occasionally entering burrows, sometimes closely following prey-laden *B. troglodytes* down their burrows.

Prey flies collected for this study were dismembered to determine their FMR, and could not be subsequently identified to any great degree.

Tachytes chrysopyga

Tachytes chrysopyga females averaged 52 ± 2.6(N = 31) mg in body mass and 18 ± 1.0(N = 31) mg in thorax mass, yielding an unladen FMR of 0.33 ± 0.007(N = 30). Prey items of *T. chrysopyga* averaged 50 ± 4.8(31) mg, producing a mean loaded FMR of 0.18 ± 0.007(N = 30) in the wasps. The latter value is very close to the
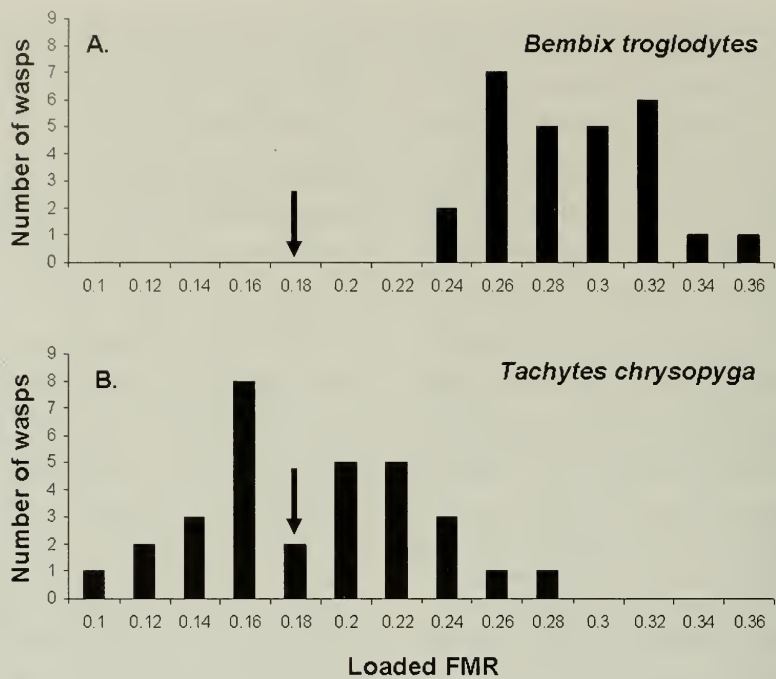
Fig. 1.   The distribution of flight muscle ratios (FMR) in wasps carrying prey. Arrows indicate the marginal flight muscle ratio, below which take-off is not possible. a. *Bembix troglodytes* from south Texas. b. *Tachytes chrysopyga obscurus* from northern Illinois.
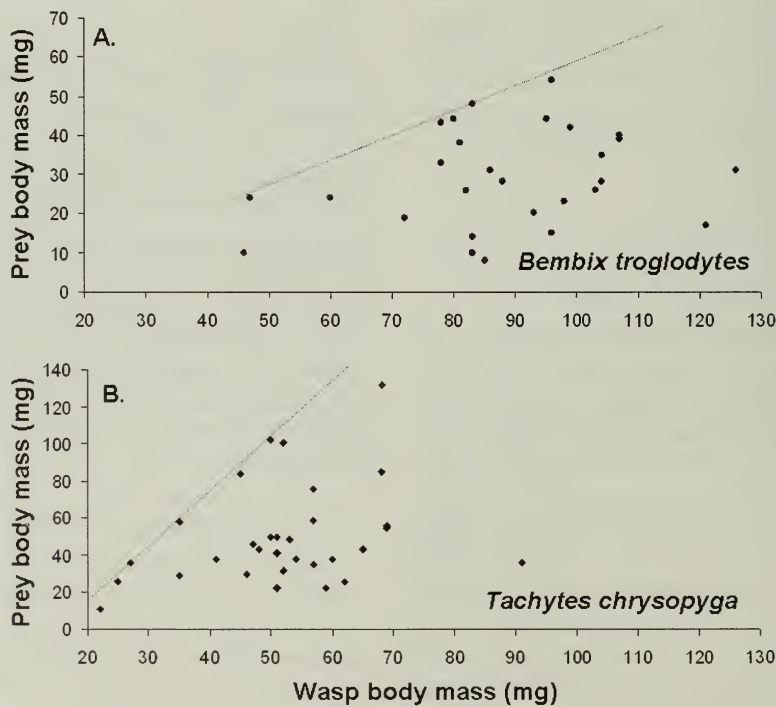

Fig. 2.   The effect of wasp size on prey size in two solitary wasps. a. *Bembix troglodytes* from south Texas. b. *Tachytes chrysopyga obscurus* from northern Illinois. The lines were fitted by eye to each graph to demonstrate the maximum prey size for wasps of a given body mass.

marginal FMR of 0.179, which lies within the 95% confidence interval of loaded FMR (0.16 to 0.19).

However, the range of prey mass (11 to 132 mg) resulted in a very broad distribution of FMRs, with many individuals far above (maximum = 0.26) and many far below (minimum = 0.099) the predicted value (Fig. 1B). At times, prey-loaded *T. chrysopyga* were fast, maneuverable and difficult to capture. However, some individuals performed short, hopping flights along the ground and were easily caught. It was very common for the females with prey to land, perhaps even releasing their prey for a few seconds, en route to their burrows. We never observed prey stealing, nor did we ever see conspecific females lurking around the burrows of others. In fact, we found small numbers of abandoned prey in the area of the nest aggregation. Although satellite flies were often observed closely trailing prey-laden *S. speciosus*, perching near and entering their burrows, we never saw evidence of such flies similarly harassing female *T. chrysopyga* in the same area.

During much of the day, many *T. chrysopyga* were flying about low to the ground, though some were certainly males. The burrows were small and relatively inconspicuous, with entranceways sometimes near that of an eastern cicada killer. There was no obvious tumulus near the *T. chrysopyga* entranceway, though the small amount of dirt could easily have been displaced by weather or other disturbances. Entranceways appeared to be open, although they could have been sealed deeper in the burrow.

Prey of *T. chrysopyga* were diverse Orthoptera, including Gryllidae (16 Enopterinae, 7 Oecanthinae), Tettigoniidae (1 Conocephalinae, 3 Copiphorinae) and Acrididae (8 Cyrtacanthacridinae). The sole adult among the prey was a meadow grasshopper (Conocephalinae).

There was no significant relationship between wasp body mass and prey body mass in *T. chrysopyga*. But, as in *B. troglodytes*, small wasps were restricted to the smallest prey, while larger wasps carried a greater range of sizes of orthopterans (Fig. 2B).

B. troglodytes was significantly larger than *T. chrysopyga* in both body mass ($P < 0.0001$, $T = -10.85$, df = 77) and thorax mass ($P < 0.0001$, $T = -12$, df = 76). Unladen FMR was significantly higher in *B. troglodytes* ($P < 0.0001$, $T = -10.25$, df = 76), as was laden FMR ($P < 0.0001$, $T = -10.25$, df = 55). However, prey mass was significantly higher in *T. chrysopyga* than *B. troglodytes* ($P = 0.0025$, $T = 3.15$, df = 62).

DISCUSSION

Bembix troglodytes

At first glance, *B. troglodytes* appears to be a suboptimal forager, at least in the context of our FMR-based model. The wasps could in theory decrease the time spent hunting and the number of hunting trips by simply capturing and carrying larger flies. This strategy would doubtless increase the number of offspring that could be reared during the wasps' short life spans, but there may be mitigating factors involved. Larger flies may be less available or more difficult, energetically expensive and time-consuming to capture. The flies that were captured had lower FMR than unladen *B. troglodytes*. FMR is a useful indicator of maneuverability (see Marden 1989, Marden and Chai 1991). Hence, *B. troglodytes* should have been able to capture the flies on the wing. Prey records for *Bembix* include fast-flying tabanids (Evans 1957).

It is possible that the foraging strategy of *B. troglodytes* minimizes prey stealing. Few wasps returning with prey made it to their burrows unchallenged, and though some of the attacking conspecifics could have been males attempting to mate, theft by females was frequent. Evans (1957) did not report prey stealing in *B. troglodytes*, but the aggregations he studied were relatively

diffuse. Ours was rather dense, which increases the likelihood of thievery or harassment by males. Evans (1957) did report prey stealing in five of ten species of *Bembix* examined. In the related wasp *Stictia heros* (Fabr.), in which prey theft is common, the probability of being attacked is directly related to the size of prey (Villalobos and Shelly 1996). These authors suggest that female *Stictia* carrying large prey were more vulnerable because of their lower flight speed and maneuverability. Therefore, if *B. troglodytes* females took larger flies, they would likely suffer greater rates of conspecific attack. Small prey help them maintain a high level of maneuverability, as we observed, and probably improve the likelihood of successful transport of the prey all the way to the burrow. *Bembix* females can compensate for small prey size by increasing the number of prey.

Tachytes chrysopyga

On first appraisal, *T. chrysopyga* appears to be an optimal forager (using our simple FMR-based model), its loaded FMR being indistinguishable from the predicted value that would maximize load carriage. On average, *T. chrysopyga* takes prey that make full use of its load-lifting capacity. However, upon closer inspection, *T. chrysopyga* is, in fact, highly variable in the size of prey it takes, and consequently, the magnitude of loaded FMR it experiences. These results are comparable to those of Elliot and Salbert (1981), who found that *T. tricinctus* (F.) prey varied from 36.3 to 214 mg, averaging 93.8 mg. These prey are about twice the size of those of *T. chrysopyga*, which is not surprising, as *T. tricinctus* females, averaging 126.5 mg, are over twice the size of *T. chrysopyga*. However, the approximately tenfold range in prey mass in both species may reflect a similarly opportunistic foraging behavior. Prey need not be exceedingly small, as prey stealing is not apparent in these species. Overloading is compensated by behavior – short, hopping flights being adequate to return some

prey to the burrow. Prey need not be exceedingly large either, as *Tachytes* provisions with a variable number of prey (Evans and Kurczewski 1966), and greater numbers could compensate for smaller size.

In spite of being ground-nesting digger wasps with many behaviors in common, *B. troglodytes* and *T. chrysopyga* provide interesting contrasts in foraging strategy. As the vast majority of its prey are flightless, *T. chrysopyga* does not require great maneuverability (bestowed by high unladen FMR) to capture them, as does *B. troglodytes*. *Bembix troglodytes* is a large wasp that takes many, small prey, while *T. chrysopyga* is a small wasp that takes fewer, larger prey (Fig. 2). Both revealed their maximum prey size, as demonstrated by the nearly straight line that can be drawn through the highest points (at a give body size) in Figs 2 A and B. For *B. troglodytes*, the maximum is somewhat below the wasp's own body mass, while for *T. chrysopyga* it is well above the wasp's body mass. In each species of wasp, the same predictions were applied and essentially the same methods used. Neither species conformed to these predictions; however, much was learned about the biology and behavior of each wasp.

ACKNOWLEDGMENTS

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